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Hodum, Peter J.; Sydeman, William J.; Visser, G. Henk; Weathers, Wesley W.

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ENERGY EXPENDITURE AND FOOD REQUIREMENT OF CASSIN'S AUKLETS PROVISIONING NESTLINGS[1]

PETER J. HODUM
Department of Avian Sciences, University of California, Davis, CA 95616-8532, e-mail: pjhodum@ucdavis.edu

WILLIAM J. SYDEMAN
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970-9701

G. HENK VISSER
Zoological Laboratory, P.O. Box 14, 9750 AA Haren, The Netherlands, and Centre for Isotope Research, Nijenborgh 4, 9747 AG Groningen, The Netherlands

WESLEY W. WEATHERS
Department of Avian Sciences, University of California, Davis, CA 95616-8532

Abstract. We used the doubly-labeled water technique to measure the field metabolic rate (FMR) of free-ranging adult Cassin's Auklets (*Ptychoramphus aleuticus*) that were provisioning half-grown nestlings. FMR averaged 3.68 ± 0.38 mL CO_2 g^{-1} hr^{-1} (n = 9), which is equivalent to a daily energy expenditure of 413 ± 59 kJ. Although Cassin's Auklet FMR is high for nonpasserines in general, it is 85% of the value predicted allometrically for a cold-water seabird that uses flapping flight. Based on stomach samples, crustaceans comprised 99.2% of the birds' diet, with euphausiids comprising 83.4% of total food items. Cassin's Auklets need to consume 67% of their body mass in euphausiids per day in order to meet their energy expenditure during chick rearing. Water flux rate averaged 872 ± 114 mL H_2O kg^{-1} day^{-1}, which is about five times that predicted allometrically. High FMR reflects the high costs of flapping flight and pursuit diving in this pelagic feeding alcid. High water flux rates may be attributed to diet and foraging mode.

Key words: Cassin's Auklets, daily energy expenditure, doubly-labeled water, field metabolic rate, food consumption, Ptychoramphus aleuticus, *seabird energetics.*

Cassin's Auklets (*Ptychoramphus aleuticus*) breed along the western boundary of North America from Baja California northward into subarctic waters (Ainley et al. 1990). They lay a single egg like most alcids, but in some locations they may raise a second clutch under favorable conditions (Ainley et al. 1990). One of the best studied Cassin's Auklet breeding colonies occurs on Southeast Farallon Island (SEFI: 37°04′N 123°00′W), California (Manuwal 1974, 1979). The Farallon Islands lie immediately east of the California Current in a highly productive region of the world's oceans. Cassin's Auklets breeding on the Farallon Islands forage in pelagic waters, with large feeding concentrations found near the continental shelf up to 50–60 km from the island (Briggs et al. 1987, Ainley et al. 1996). They are one of the most abundant breeding birds on SEFI, with an estimated population of approximately 20,000 pairs.

Cassin's Auklets are strictly nocturnal in their visits to the nest which, in conjunction with their need to travel to distant offshore foraging grounds, limits breeding birds to one return-trip per night to feed their chick (Manuwal 1974). In this study, we measured field metabolic rate (FMR) and estimated adult daily food consumption of Cassin's Auklets feeding nestlings. Previous studies of alcid FMR have examined only high-latitude populations and it is unclear how FMR might vary regionally. Because the Farallon Islands population of Cassin's Auklets inhabits a cold water oceanographic regime, we hypothesize that their FMR should be similar to that of other alcid populations despite their lower latitude.

METHODS

We determined Cassin's Auklet FMR between 7–19 June 1993 using the doubly-labeled water (DLW) technique (Tatner and Bryant 1989). The birds we measured were part of a long-term demographic study, had individual metal leg-bands, and nested in artificial burrows (i.e., nest boxes). All experimental nests were at the post-guard stage of the breeding cycle, during which both parents leave the chick unattended by day to forage at sea. Chicks were approximately 10–15 days old, which is within the period of maximal growth (Ainley et al. 1990). Mean fledging age is 42 days (Ainley et al. 1990). Parents returned to the island at night to feed their chick and departed again early the next morning before sunrise (day length was approximately 15 hr during our study). We used both parents in six pairs of breeding auklets for our study. Each pair's chick was growing normally at the time of the experiment and subsequently fledged. After adults entered nest boxes we blocked the entrances at ap-

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TABLE 1. Body mass, field metabolic rate (FMR), and water efflux of Cassin's Auklets provisioning nestlings.

Bird	Sex	Mean mass (g)	Mass change (%)	FMR		Water efflux
				(mL CO_2 g^{-1} hr^{-1})	(kJ day^{-1})	(mL H_2O kg^{-1} day^{-1})
1	M	202.2	−13.6	3.61	470	873
2	F	169.1	−4.8	3.52	383	867
3	F	160.5	−4.8	3.16	326	1,028
4	F	177.2	−7.7	4.22	481	1,020
5	M	170.0	−3.2	3.65	399	733
6	F	176.9	−4.2	3.41	388	733
7	M	177.7	−4.7	4.44	507	845
8	M	154.5	−1.5	3.39	337	998
9	M	177.8	−1.9	3.73	426	748
Mean ± SD		174.0 ± 12.7	−5.2 ± 3.1	3.68 ± 0.38	413 ± 59	872 ± 114

proximately 22:30. We allowed parents time to feed their chick then captured them between 01:00–03:00, recorded their weight, and measured their bill depth. Birds with a bill depth > 10.3 mm were assumed to be male, those with a depth < 10.3 mm, female (Nelson 1981). Overall, only 15% of birds overlap in bill depth. Because we worked with marked pairs and because there was no overlap in bill depth between members of a pair, we are confident that we sexed birds correctly. Each bird was injected intraperitoneally with 0.18 mL of water containing 63 atoms percent ^{18}O and 33 atoms percent ^{2}H, held for 1 hr to allow the injectate to equilibrate with body water (Degen et al. 1981, Williams and Nagy 1984), blood sampled (ca. 40 μL collected from a brachial vein), and then released. Birds were recaptured about 48 hr later upon their return from a foraging trip, reweighed, and a second blood sample obtained (mean ± SD interval between blood samples was 1.96 ± 0.02 days, range 1.95–2.01). Thus the measurement period reflects FMR over two foraging trips. We recaptured 11 of 12 birds injected (one individual did not return to the nest during the recapture evening), but only 9 birds contained sufficient isotopes to permit calculation of FMR. Blood samples were stored in flame-sealed hematocrit tubes until analyzed for $^{18}O/^{16}O$ and $^{2}H/H$ ratios at the University of Groningen, The Netherlands. We calculated rates of water efflux and CO_2 production from isotope turnover using the equations of Lifson and McClintock (1966) as modified by Nagy (1975), and calculated body water volume from ^{18}O dilution following Nagy and Costa (1980). We converted CO_2 production to energy expenditure in kJ day^{-1} assuming an energy equivalent of 26.8 J per mL CO_2 (Ricklefs et al. 1986).

Ideally, background isotope levels should be determined for each animal prior to injection with labeled water, especially in studies employing low ^{18}O enrichment. This increases both handling time and disturbance to the animal, however, and is not commonly done. We determined natural background isotope abundance in five uninjected adult auklets. Background isotope levels averaged 0.13 ± 0.53 delta per mil (range −0.25 to 1.17) for ^{18}O and −9.74 (3.54 delta per mil (range −14.25 to −4.35) for ^{2}H. We used these mean background levels in our CO_2 production calculations. Using an estimated background level rather than the bird's actual level can introduce significant errors when final isotope levels are near background (Tatner 1990), as was the case for ^{18}O in our study (final ^{18}O level averaged 15.5 delta per mil). We assessed the error that this might introduce in our study by calculating each bird's CO_2 production five times, once for each of the five different background ^{18}O levels. The maximum difference in CO_2 production ranged from −17% to +29%. It seems likely that individual CO_2 values may be in error by this much. The error in mean CO_2 production for the nine recaptured auklets should be much smaller than this, however, as the background ^{18}O level of individual birds should vary randomly. Values are reported as mean ± SD.

RESULTS

FIELD METABOLIC RATE AND WATER FLUX

We combined data for males and females because there were no significant differences between the sexes in body mass ($t_8 = -0.77$, $P > 0.05$), FMR ($t_8 = 0.40$, $P > 0.05$), water efflux ($t_8 = 1.37$, $P > 0.05$), or mass loss ($t_8 = -0.12$, $P > 0.05$). Cassin's Auklet FMR averaged 3.68 ± 0.38 mL CO_2 g^{-1} hr^{-1} during the 48-hr measurement interval and body mass averaged 174.0 ± 12.7 g (Table 1). Although all nine birds lost some mass during the 2-day measurement interval, 7 of 9 birds lost < 5% mass, and mean mass loss was 5.2 ± 3.1% (Table 1). There was no relationship between FMR and mass loss during the measurement interval ($r^2 = 0.26$, $P > 0.05$); birds that lost more mass were not more likely to have higher FMR values. Water efflux of Cassin's Auklets averaged 872 ± 114 mL H_2O kg^{-1} day^{-1} or 152 mL H_2O day^{-1}. There was no relationship between FMR and water flux ($r^2 = 0.19$, $P > 0.05$).

DIET

Fish comprised less than 1% of prey items in Cassin's Auklet diet samples. Crustaceans comprised 99.2% of the 3,487 individual prey items identified during the 1993 chick-rearing period (Sydeman et al. 1997). Euphausiids were the dominant crustacean consumed. They comprised 83.4% of total food items and consisted of three species: *Euphausia pacifica, Nyctyphanes simplex,* and *Thysanoessa spinifera.* Mysid shrimp comprised 14.6% of the diet items, decapods 1.1%, and amphipods 0.1%.

DISCUSSION

An El Niño Southern Oscillation (ENSO) event that began early in 1992 and persisted through 1993 influenced oceanographic conditions during our study. The event appeared to delay the annual phytoplankton bloom, reduced apparent overall prey availability, and altered the distribution and abundance of zooplankton prey, particularly euphausiids (Lenarz et al. 1995). As a consequence, the 1993 Cassin's Auklet breeding season on SEFI was delayed and productivity was below normal (W. J. Sydeman, unpubl. data). How this event may have affected auklet FMR is uncertain, but our data may differ from those of non-ENSO years.

The rate of CO_2 production we measured corresponds to a daily energy expenditure of 413 ± 59 kJ. The amount of food that Cassin's Auklets would need to consume to meet this energy requirement can be calculated from the type and energy content of ingested prey. Based upon an average energy density of 4.65 kJ g^{-1} for krill (Nicol et al. 1995), and assuming an assimilation efficiency of 76% (Montevecchi et al. 1984), we estimate that Cassin's Auklets need to consume 117 g of euphausiids per day (approximately 67% of their body mass) in order to meet their energy demands. This result can be compared with those of prior studies of alcids feeding chicks. Black Guillemots *Cepphus grylle* feeding on fish consumed 61% of their body mass in prey per day (Mehlum et al. 1993), whereas the small, high-arctic breeding Dovekie *Alle alle* had to consume prey equaling 80% of its mass per day to meet its proportionately higher FMR (Gabrielsen et al. 1991). Cassin's Auklets and Dovekies are both planktivorous and quite similar in body size. The pronounced difference in their prey consumption rate reflects differences in their patterns of chick provisioning. Cassin's Auklets are nocturnal at the colony and typically make a single round-trip from foraging area to chick per day. Dovekies, in contrast, are active throughout the 24-hr daily cycle and make up to 10 round-trips between the feeding grounds and chick each day. Presumably Dovekies allocate more energy to foraging than Cassin's Auklets, but this may permit them to bring more food to their chicks as nestling Dovekies develop more rapidly than Cassin's Auklets (Ainley et al. 1990).

Our food consumption estimate assumes a diet composed exclusively of euphausiids, which is reasonable as fish rarely compose a large proportion of the diet (Ainley et al. 1990, 1996). Given these estimates, the Farallon Islands breeding population of adult Cassin's Auklets would consume approximately 4,440 kg of euphausiids per day to meet their energy requirements during the chick-rearing period. The total amount of krill harvested by the SEFI population would be even greater than this, however, because our estimate does not include krill consumed by dependent chicks.

Cassin's Auklets had a high rate of water efflux; 5.2 times that predicted for nonpasserine birds in general (Nagy and Peterson 1988) and 3.1 times that predicted for mostly aquatic birds with salt glands (Hughes et al. 1987). Water efflux in diving Tufted Ducks (*Aythya fuligula*) also is relatively high (Bevan et al. 1995); 6.5–13 times that predicted allometrically by Nagy and Peterson's (1988) equation (de Leeuw 1997). High

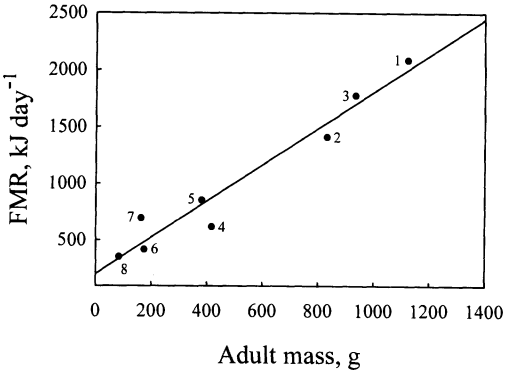

FIGURE 1. Field metabolic rate (FMR) determined by doubly-labeled water in six species of alcids. Numbers correspond to species in Table 2. See text for regression equation.

rates of water flux in Cassin's Auklets and Tufted Ducks compared with birds in general reflect their diet and foraging mode. Auklets, like Tufted Ducks, capture invertebrate prey underwater, and thus presumably ingest water that is attached to the prey. Additionally, seabirds tend to have high daily energy expenditures, thereby resulting in high food intake levels with an associated increased ingestion of seawater. The high water content of prey items also contributes to a high water turnover rate.

Eight studies of at-sea alcid FMR have employed the DLW method, including two pairs of studies that looked at different populations of the same species (Fig. 1, Table 2). In each of these studies the adults were provisioning chicks although chick age was not reported in five of the studies. In the other three studies, chicks were all in the first third of the nestling period. Assuming each of the eight populations to be an independent estimate, alcid FMR can be described by the equation

$$y = 206.4 + 1.60x$$

$$(r^2 = 0.948,\ s_{yx} = 160.8,\ s_b = 0.15,\ n = 8)$$

where y is FMR in kJ day^{-1} and x is body mass in grams. This equation predicts an FMR of 1,006 kJ day^{-1} for a hypothetical 500-g alcid, whereas the comparable prediction for a nonpasserine bird is 504 kJ day^{-1} (Nagy 1987, Eq. 7). Seabirds have relatively high FMRs, however, and the FMR predicted for a 500-g cold-water seabird is higher, 862 kJ day^{-1} (Birt-Friesen et al. 1989). Alcid FMR corresponds closely with predictions for cold-water seabirds that use flapping flight, 1,006 vs. 1,050 kJ day^{-1} for a 500-g bird (Birt-Friesen et al. 1989). On average, the FMR of alcids is 5 ± 23% higher than that of other cold-water seabirds using flapping flight (Table 2). The average deviation from predicted (ignoring sign) is 18%.

The relatively high FMR of alcids compared with that of nonpasserines in general likely results from their flight style and foraging mode (Birt-Friesen et al. 1989, Adams et al. 1991). Nagy et al. (1984) found

TABLE 2. Comparison of field metabolic rate (FMR), determined by doubly-labeled water, of alcids provisioning nestlings with predicted values for cold-water seabirds using flapping flight (Birt-Friesen et al. 1989).

Species		Mass (g)	FMR (kJ day^{-1})	Predicted FMR (kJ day^{-1})	% deviation from predicted	Source[a]
Thick-billed Murre	*Uria lomvia*	1,119	2,080	1,886	10	1
		834	1,413	1,523	−7	2
Common Murre	*Uria aalge*	940	1,789	1,661	8	3
Black Guillemot	*Cepphus grylle*	420	621	925	−33	4
		380	860	860	0	5
Cassin's Auklet	*Ptychoramphus aleuticus*	174	413	487	−15	6
Dovekie	*Alle alle*	164	696	467	49	7
Least Auklet	*Aethia pusilla*	84	358	287	25	8

[a] (1) E. Flint, unpubl. data, (2) A. Gaston, unpubl. data, (3) Cairns et al. (1990), (4) A. Gaston, unpubl. data, (5) Mehlum et al. (1993), (6) this study, (7) Gabrielsen et al. (1991), (8) Roby and Ricklefs (1986).

that pursuit diving in Jackass Penguins (*Spheniscus demersus*) was an energetically expensive foraging method and concluded that there were differences in relative energy costs between various foraging modes. Alcids, which also utilize pursuit diving, have a reduced wing area and wing span compared to other flying seabirds (Pennycuick 1987), resulting in a wing shape that optimizes neither flight nor diving efficiency. Roby and Ricklefs (1986) compared energy expenditure rates of pursuit-diving seabirds with species having different foraging modes and concluded that the power requirements for flight in pursuit divers were twice those of aerially foraging seabirds.

The relative energy cost to adults of foraging and food transportation must be considered when evaluating reproductive patterns in seabirds (Ricklefs et al. 1986). One-chick broods typical of most alcids may be a consequence of the high energy cost of flight and pursuit diving (Roby and Ricklefs 1986). Black Guillemots, which are inshore feeders, are able to raise successfully two chick broods because the higher energy demand of rearing a larger brood may be compensated by the decreased energy cost of inshore foraging (Mehlum et al. 1993). Conversely, energetically expensive long-distance foraging strategies by other alcid species may preclude successful two-chick broods.

Despite raising only one chick per clutch, Cassin's Auklet mass specific energy expenditure (3.68 ± 0.38 mL CO_2 g^{-1} hr^{-1}) is similar to that of Black Guillemots (3.63 ± 0.74 mL CO_2 g^{-1} hr^{-1}) provisioning two chicks (Mehlum et al. 1993). Cassin's Auklets are much smaller than Black Guillemots, however, and therefore would be expected to have a higher specific metabolic rate. The difference in size between the two species can be accounted for by comparing their FMRs with allometric predictions. Cassin's Auklet FMR was 85% of that predicted for a cold-water seabird that utilizes flapping flight (Birt-Friesen et al. 1989). The two studies of Black Guillemot FMR reported divergent results, 67% (A. Gaston, unpubl. data) and 100% (Mehlum et al. 1993) of predicted FMR (Table 2). Cassin's Auklet FMR as a percentage of predicted, therefore, overlapped Black Guillemot values despite the difference in clutch sizes. FMR of other alcids showed no clear pattern with respect to allometric predictions, although two of the smaller species, Least Auklets and Dovekies, had the highest FMRs (Table 2).

Compared with nonpasserines and seabirds in general, Cassin's Auklets and other alcids have higher energy costs than allometrically predicted, presumably because of the high energy cost of flight and foraging and the need to commute between the breeding colony and offshore foraging grounds. Our results are consistent with predictions that increased costs of flight and foraging in offshore feeding alcids constrain them to single-egg clutches and indicate that for Cassin's Auklets water temperature has a greater effect on FMR than latitude.

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